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Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (North and Mid-Atlantic)

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Fish and Wildlife Service
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Coastal Ecology Group
Waterways Experiment Station
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Performed for

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Vicksburg, MS 39180

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Fish and Wildlife Service
Research and Development
National Wetlands Research Center
Washington, DC 20240

PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

Suggestions or questions regarding this report should be directed to one of the following addresses.

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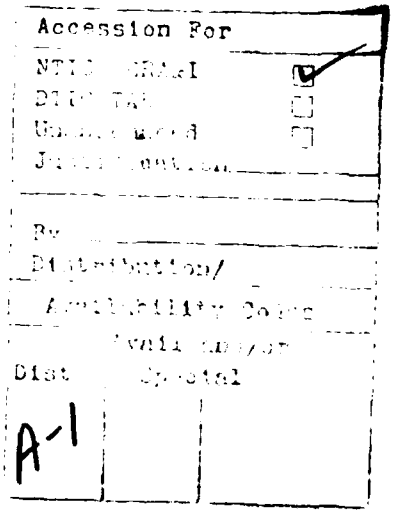

CONVERSION TABLE

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters (m)	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers (km)	0.5396	nautical miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters (m^3)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons (t)	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (°C)	1.8(°C)+32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	[illegible]
statute miles (mi)	1.609	[illegible]s
nautical miles (nmi)	1.852	[illegible]rs
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28350.0	milligrams
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
pounds (lb)	0.00045	metreic tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (°F)	0.5556 (°F-32)	Celsius degrees

CONTENTS

ACKNOWLEDGMENTS

The blue mussel, Mytilus edulis, is often considered to be the "white rat" of the marine invertebrate zoologist, due to its widespread distribution and the ease with which it can be collected and maintained in the laboratory. As a consequence it has been the subject of intense scientific investigation over the last two decades. This wealth of information has made my task of assembling this brief review of the biology of the blue mussel on the Atlantic coast of the United States particularly challenging. Therefore, within the text I have referenced the major reviews of various aspects of the biology of the blue mussel where interested readers can obtain more detailed information. In particular, I draw attention to the book Marine Mussels, edited by Bayne (1976a), which provides a comprehensive treatment of many aspects of the biology of Mytilus edulis.

I am grateful to Dr. Thomas J. Hilbish, Dr. Victor S. Kennedy, Mr. Carter Newell, and Dr. Ray J. Thompson for reviewing a draft of this manuscript. Debbie Kennedy drew the illustration of the blue mussel shell.

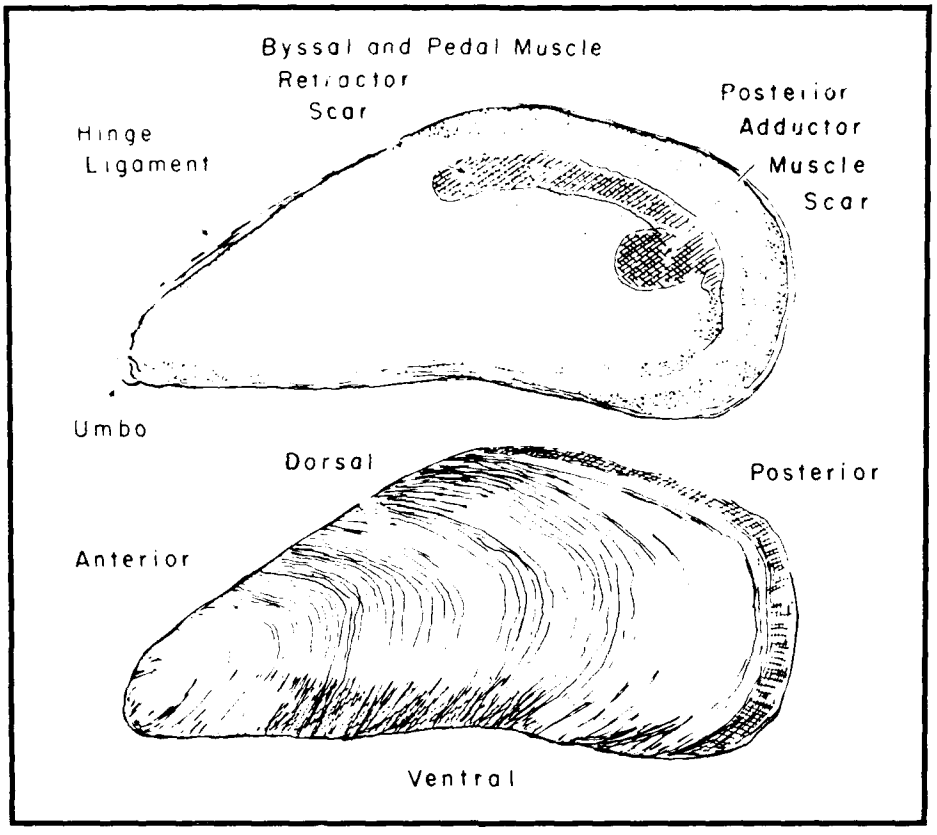

Figure 1. Internal and external characteristics of the blue mussel Mytilus edulis.

BLUE MUSSEL

NOMENCLATURE, TAXONOMY, AND RANGE

Scientific name.....Mytilus edulis Linne 1758 (Abbott 1975)
Preferred common name .....blue mussel (Figure 1)
Other common names..... mussel, sea mussel
Class .....Bivalvia (Pelecypoda)
Order.... .....Mytiloida
Family.....Mytilidea

Geographic range: The blue mussel is a widely distributed boreo-temperate species occurring in the Arctic, North Pacific, and North Atlantic Oceans (Seed 1976). On the east coast of North America, its range extends from Labrador to Cape Hatteras, North Carolina (Wells and Gray 1960), and it is common throughout the North Atlantic and Mid-Atlantic Regions (Figures 2 and 3). It is most common in the littoral to sublittoral zones (<99 m) of oceanic and polyhaline to mesohaline estuarine environments; however, it has been found in deeper and cooler waters (100 to 499 m) that enable it to penetrate as far south as Charleston, South Carolina (Theroux and Wigley 1983).

MORPHOLOGY AND IDENTIFICATION

The shape of the blue mussel shell is roughly an elongate triangle; the longest dim-

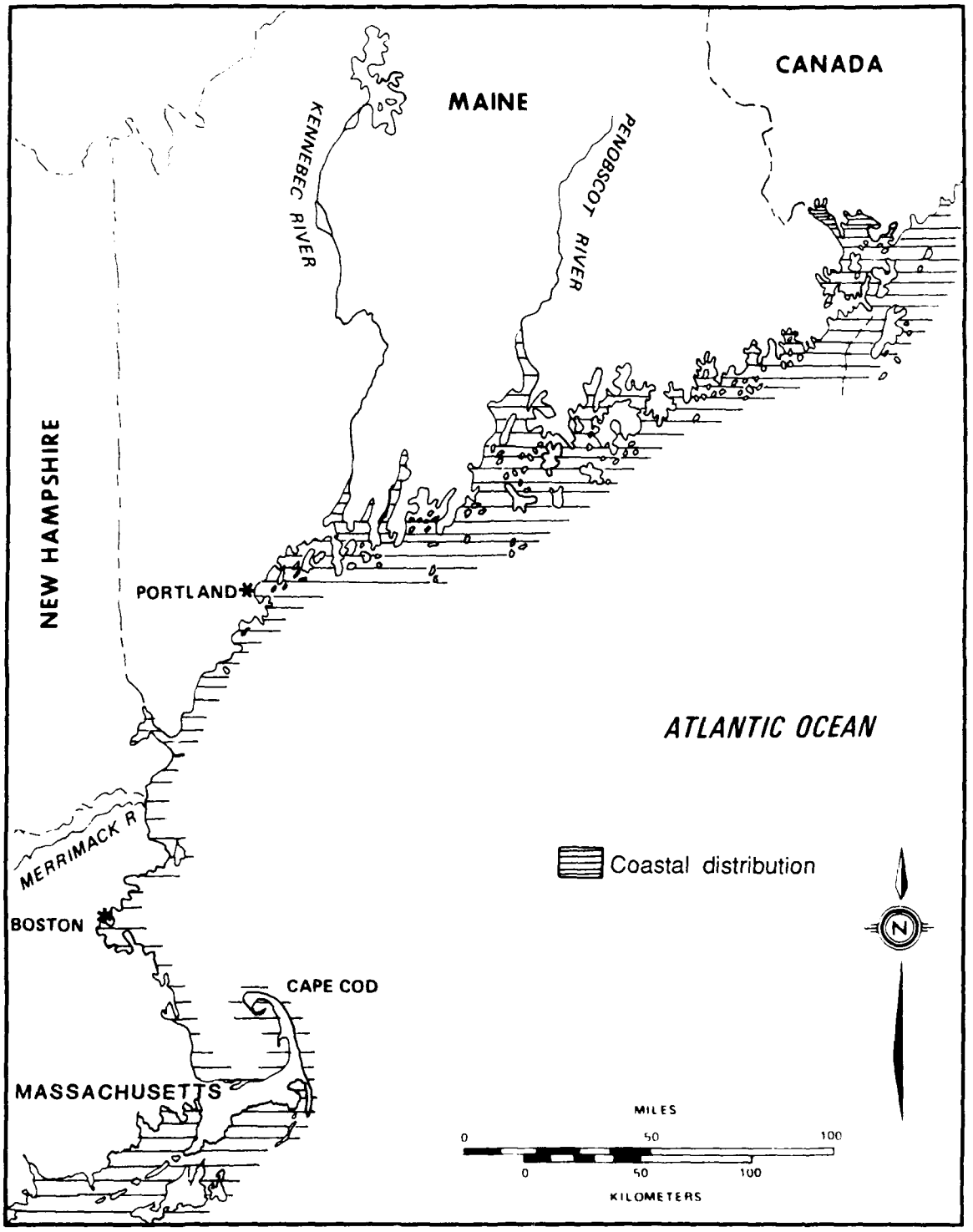

Figure 2. North Atlantic distribution of the blue mussel.

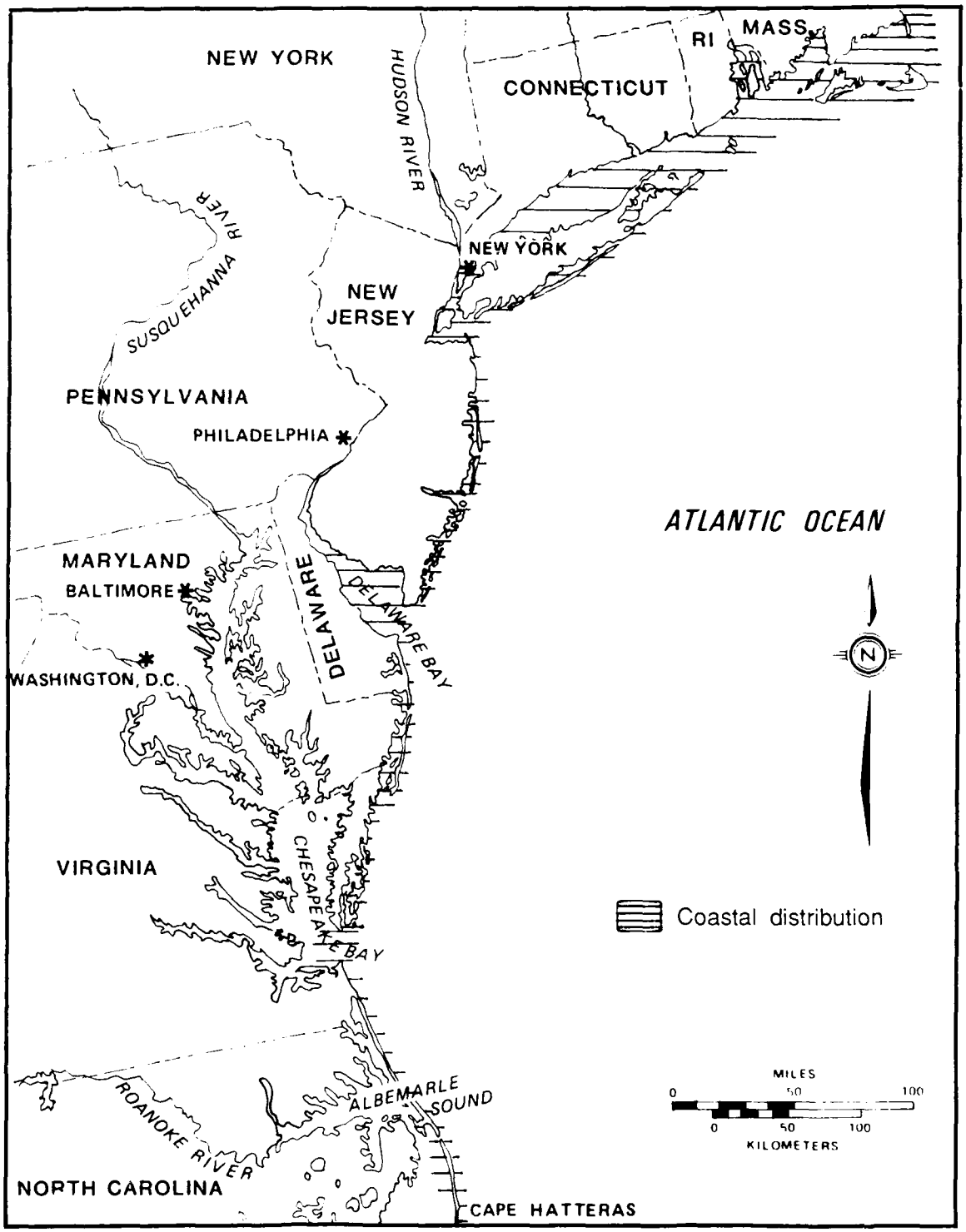

Figure 3. Mid-Atlantic distribution of the blue mussel.

ension (ca. 7-10 cm) is along an anterior-posterior axis from the narrow beaks of the umbo to the broad posterior shell margin (Figure 1). The shell has a sculpture of fine concentric lines and is dark blue to black in color. The entire outer surface of the shell is covered by a shiny proteinaceous membrane, the periostracum. As this protective periostracum becomes abraded, especially toward the umbo, the outer, colored, prismatic calcitic layer sometimes becomes eroded, exposing the white, inner, prismatic, aragonitic layer (Carter 1980). Within any blue mussel population, a few individuals have shells that are light brown or have stripes of different shades of brown. The interior of the shell has a border of dark blue to violet surrounding the pearly white nacreous layer.

Blue mussels are semi-sessile epibenthic bivalves that are anchored to a secure substrate, or attached to other mussels, with byssus threads secreted from glands in the animal's foot. When the valves are closed, the byssus threads pass through a small notch, the pedal gape, in the middle of the ventral junction of the two valves. The blue mussel can achieve a limited degree of movement by secreting new threads and adjusting the lengths of others. This mobility enables the animal to reposition itself in relation to water currents (Yonge 1976), to avoid getting smothered by accreting sediments (Seed 1976), and to move toward the outer edge of mussel clumps (Harger 1968).

The interior anatomy has distinctive characteristics. The posterior adductor muscle is much larger than the anterior adductor muscle. In empty shells, the scars of the posterior adductor muscle and retractor muscles (both posterior pedal and byssal [Yonge 1976]) are clearly visible (Figure 1). In the center of the visceral mass is the darkly pigmented foot, which can be extended to secrete a new byssus thread. The mantle, which extends from either side of the visceral mass, is attached to the entire periphery of both valves of the shell. New shell growth is initiated from the mantle margin (Wilbur and Saleuddin 1983). In two places posteriorly, the mantle is modified to form an inhalant and exhalent siphonal aperture to direct feeding currents into and out from the mantle cavity.

Blue mussel larvae can be identified on the basis of both their shell morphometrics and the position of the ligament (for review and photomicrographs, see Bayne 1976b). More positive larval identification can be obtained by scanning electron microscopic examination of the dentition on the hinge, which is distinctly different from that of other bivalve larvae (Lutz and Hidu 1979).

The only species within the North and Mid-Atlantic Region that can easily be mistaken for the blue mussel is the horse mussel, Modiolus modiolus. Unlike the blue mussel, the horse mussel has umbonal beaks, which are not at the apex of the shell but displaced to one side, and by its larger adult size (10-15 cm) and heavier and more eroded shell. Juvenile horse mussels can be distinguished from blue mussels by periostracal "hairs" on the posterior margin of the shell. The horse mussel is usually found in deeper oceanic water than the blue mussel and does not penetrate estuaries. The shells of other species of mussels, such as the ribbed mussel, Geukensia demissa, and the hooked mussel, Brachidontus recurvus, have numerous ridges radiating from the umbo towards the posterior shell margin that clearly distinguish them from the smooth shell of the blue mussel.

REASON FOR INCLUSION IN SERIES

The blue mussel is a common and often abundant species in the coastal waters of the North and Mid-Atlantic Regions, where it is an important prey item for many animals. Unfortunately, it is precisely these waters that are affected most by the increased urbanization of the Northeastern United States and the disposal of industrial wastes. In addition to its ecological importance, the blue mussel is currently the basis of a resurgent fishery based on wild stocks and a developing aquaculture industry throughout the North Atlantic Region.

LIFE HISTORY

Reproductive Physiology

The blue mussel is diecious, though rare instances of hermaphroditism have been

reported (Seed 1976). Mussels generally produce gametes and are ready to spawn by the time they are one year old; however, when adverse environmental conditions (e.g., prolonged periods of exposure to air) cause a slow rate of growth, sexual maturity is sometimes not attained until the second year.

Although the gonad is situated within the visceral mass it extends during the reproductive period into the mantle, which also becomes swollen with gametes. Previtellogenesis (i.e. formation of oogonia and spermatogonia) occurs during the period from winter through early spring when food availability is generally low and feeding activity is further depressed by low water temperatures. Energy for gametogenesis during this period is supplied from nutrient reserves of glycogen, which are sequestered during the post-spawning period and stored in the vesicular cells specialized cells in the connective tissue of the mantle (reviewed by Gabbott 1983). The blue mussel sequesters a separate nutrient reserve in the digestive gland to supply the energy that sustains metabolic energy demands during the period of reduced food intake in the winter. Vitellogenesis, the final stage of gametogenesis when the spermatocytes and oocytes are formed, usually occurs over a comparatively short period of a few weeks in the late spring, during which the nucleus enlarges and lipids are synthesized and stored in the egg yolk (for review see Sastry 1979). Energy for vitellogenesis is supplied from the remaining glycogen reserves, from lipid reserves stored in adipogranular cells in the mantle, and from freshly ingested food material (Gabbott 1983). The ripe gametes are then ready to be spawned; if their release is delayed, they degenerate and are resorbed by hemocytes.

Gametogenesis, spawning, and nutrient storage are linked in an integral process termed the reproductive cycle. This cycle in any blue mussel population is the result of a complex balance between exogenous factors such as food availability, temperature, salinity, and duration of exposure to air and endogenous factors such as nutrient reserves, hormonal cycle, and genotype (Seed 1976; Sastry 1979). Interaction between these factors ensures the synchrony of gamete development within the population. Such synchrony is essential for an oviparous species and ensures that larvae are in the water at the optimum time for their growth and survival (Sastry 1979).

The timing of the various components of the reproductive cycle differs greatly between various blue mussel populations within the North Atlantic and Mid-Atlantic Regions (Figure 4: Newell et al. 1982). Newell et al. (1982) concluded that latitude and water temperature were not as important as food availability in governing the reproductive cycle of the blue mussel along the east coast of the United States. Thus, it is impossible to predict the timing of the reproductive cycle for any particular population. For environments in which variations in physical factors are not large -- especially those that influence patterns of phytoplankton production - it is likely that the reproductive cycle for the blue mussel is probably rather constant from year to year (Newell et al. 1982). In habitats where annual variations in environmental factors are large, such as in estuaries with annually variable freshwater inputs and year to year variations in water temperature, the reproductive cycle of Mytilus edulis can be expected to vary (Thompson 1979,1984a; Lowe et al. 1982).

Spawning

When sperm and eggs are fully ripe they are released from the follicles in each gonad into a series of genital canals that gradually combine into a common gonoduct that opens on the genital papilla (Bayne 1976b). Eggs and sperm are liberated via the exhalent siphon directly into the water column, where fertilization occurs. About 10,000 spermatozoa are shed for each ovum spawned (Thompson 1979).

The exact factors that stimulate the first mussels within a population to spawn are unknown. However, a prerequisite is the presence of fully-ripe gametes that are ready to be liberated. If the gametes are ripe, spawning may be stimulated by a slight increase in water temperature or change in salinity, mechanical disturbance as a result of wave action, desiccation, or even high concentrations of phytoplankton in the water (Seed 1976). Males generally start to spawn

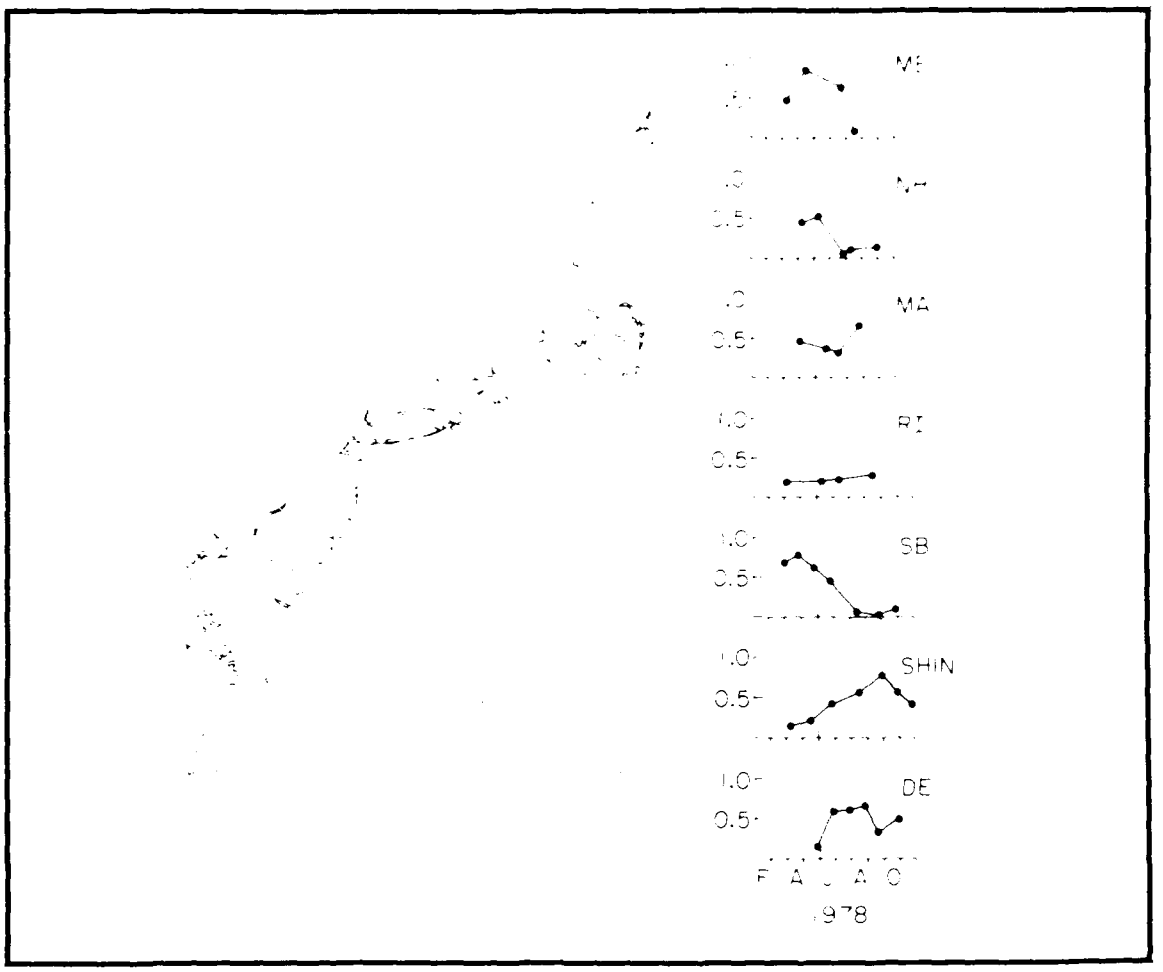

Figure 4. Mean reproductive condition of male and female blue mussels through the breeding season, measured at times designated by solid circles, from seven sites on the east coast of the United States. The reproductive condition varies between 1.0 for a fully ripe mussel and 0.0 for one with no discernible gametes. ME = Damariscotta River, Maine; NH = Newcastle, New Hampshire; MA = Cape Cod Canal, Massachusetts; RI = Narragansett Bay, Rhode Island; SB = Stony Brook, New York; SHIN = Shinnecock, New York; DE = Broadkill Inlet, Delaware (from Newell et al. 1982).

first; the presence of sperm in the water then stimulates the females to cease filtering (Newell and Thompson 1984) and start spawning. This synchronous spawning ensures that the sperm and eggs are in the water column concurrently.

At some localities, a particular set of environmental conditions enables the blue mussel to repeatedly spawn (Lowe et al. 1982; Newell et al. 1982; Rodhouse et al. 1984). Such spawnings may take the form of mass spawnings in which an individual mussel liberates most of its gametes over a short period. Such spawning is followed by a refractory period, during which further oocytes and spermatocytes are developed for the next spawning. In other situations, no large numbers of gametes in any one mussel ripen simultaneously; instead, gametes are continually ripening and are liberated in a "dribble" spawn.

Fertilization requires dribble-spawning from a number of individuals within the population.

Gametes and Fecundity

The eggs are spherical and 68-70 μm in diameter; each possesses a vitelline coat 0.5-1.0 μm thick, and contains numerous lipid droplets and yolk granules (for review see Bayne 1976b). Accurate measurements of fecundity are difficult to obtain due to the experimental difficulties of assessing an individual female's output over the entire breeding period. Estimates obtained by inducing females to spawn in the laboratory suggest that a large adult mussel (4-5 cm long) weighing 1 g (tissue dry weight) may liberate about 8×10^6 eggs (Bayne et al. 1978; Thompson 1979). More accurate fecundity estimates were obtained by Thompson (1979) from the mantle weight loss of mussels at three locations on the east coast of North America, including Stony Brook, Long Island, which indicate total fecundities per gram dry tissue weight of 1×10^7 eggs for females and 1.1×10^{11} sperm for males.

Spermatozoa swimming freely in the water column react on contact with the egg by extruding an acrosome filament (Bayne 1976b) that enables the sperm to penetrate the vitelline coat and initiate meiosis. At 18 °C the eggs hatch about 5 h after fertilization to produce a ciliated embryo.

Reproductive Strategy

The large number and small size of eggs produced by the blue mussel are typical of the planktotrophic reproductive strategy in which output is maximized but nutrient investment per egg is small (for review see Bayne 1976b). This strategy is generally considered to aid dispersal as it allows mussels to produce the maximum number of larvae which require a prolonged planktonic development period. However, such a strategy produces an egg with the barest minimum of nutrient reserves to enable the larva to develop sufficiently to start feeding on plankton.

Laboratory experiments of Bayne et al. (1975, 1978) demonstrated that the viability of mussel larvae is compromised if the parent is stressed (e.g., by high temperature, insufficient food, or pollutants) during gametogenesis and vitellogenesis. Such reduction in larval viability is most likely due to less lipid reserves being apportioned to each egg. If the adult mussels are stressed during the reproductively quiescent period or during the early stages of gametogenesis, the normal gametogenic cycle is not initiated (Bayne et al. 1982). Mussels that are stressed when ripe gametes are present begin resorbing the gametes (Bayne et al. 1982). Thus, a perturbation of an environmental factor can reduce the reproductive capacity of a blue mussel population, even though it occurs outside of the normal reproductive season and does not appear to have any adverse effects on the adult.

Larval Development and Behavior

The stages of larval development and their durations are summarized in Table 1. It must be emphasized that the larval stage may last anywhere from 15 to 35 days and that the duration is dependent on prevailing environmental conditions. Larvae of blue mussels from Connecticut developed normally only within the temperature range of 15-20 °C; at 15 °C they developed normally in salinities ranging from 15 to 35 ppt, whereas at 20 °C they could only develop normally between 20 and 35 ppt (Hrs-Brenko and Calabrese 1969). Bayne (1965) reported that the trochophore could develop successfully only in a salinity of 30-40 ppt and at temperatures of 8-18 °C, and that within this temperature range, the development rates were fastest at the highest temperatures. Larvae from an oceanic blue mussel population grew fastest at 30-32 ppt and did not grow well at salinities below 24 ppt (Bayne 1965). In contrast, larvae reared from blue mussels collected from a more estuarine population continued to develop in salinities as low as 14 ppt. Innes and Haley (1977) reported that in blue mussels, the expression of population and family differences in growth rate depended on the salinity at which the larvae were reared. They interpreted these results to indicate that there was a significant genotype-environment interaction during larval development.

These data on the influence of temperature and salinity on larval growth demonstrate that larvae are clearly influenced

Table 1. Life stages and characteristics of the blue mussel (Bayne 1976b).

Stage	Size (length)	Age and characteristics
Fertilized egg	68-70 μm	0-5 h Non motile.
Trochophore	70-110 μm	5-24 h Ciliated and motile.
Veliger		Up to 35 days; Feeds and swims with ciliated velum.
a) Prodissoconch I	110-	Straight-hinged shell.
b) Prodissoconch II	-260 μm	Umbo on shell.
c) Eyed Larvae	220-260 μm	Development of pigmented 'eye spots'.
d) Pediveliger	260 μm	Development of foot.
Plantigrade	0.26-1.5 mm	Up to 6 months; temporarily attached to filamentous substrates.
Juvenile		Up to 2 years; sexually immature.
Adult	Up to 100 mm	Up to 20 years; sexually mature.

by the environmental regime of the parent. There is some evidence to suggest that environmental variables interact to affect survival and growth (Bayne 1983). Also, tolerance to environmental variation is lower in the earlier than later larval stages, and lower in the larvae than the adult. Bayne (1976b) suggested that the environmental requirements for embryonic development are a limiting factor regulating the distribution of estuarine blue mussel populations.

The first developmental stage is the ciliated embryo which differentiates within about 24 h of fertilization to form the trochophore. Although the trochophore is motile at this stage, it is non-feeding and thus still relies on the yolk for nutrient. The veliger stage is characterized by the development of a functional mouth and alimentary system, together with a group of cilia at the anterior end that enlarge to form the velum. The ciliated velum serves both to propel the larva and to filter food particles, especially nanoplankton. A shell gland secretes a thin transparent shell, producing the characteristic "straight hinge" of the prodissoconch I shell. The veliger continues to develop and eventually the cells of the mantle assume their adult role in shell formation with the initial production of the prodissoconch II shell, characterized by the development of a pronounced umbo on the larval shell. The later stages of veliger development are characterized by the formation of a pair of photosensitive pigmented eye spots and an elongated foot with a byssal gland.

Once the velum is fully developed, the beating of the large marginal cilia on the velum can pull the larva spirally upwards through the water column. If the larva withdraws the velum into the shell or reduces the rate of ciliary beating, it sinks. The veliger is carried passively with ocean and estuarine currents because it has little ability to swim horizontally. However, the larvae of many bivalves (Mileikovsky 1973), including those of Mytilus edulis (Bayne 1963, 1964), alter their swimming behavior in response to certain key environmental stimuli such as salinity, gravity, pressure, and light. Generally, the responses by younger larvae to environmental factors keeps them in surface waters. Older larvae tend to sink to the bottom in response to reduced salinity but swim upward in response to increasing salinity. Such behavioral responses have generally been interpreted as indicating that larvae of estuarine species respond to the reduction in salinity that occurs in estuaries on the ebb tide by dropping out of the net seaward-moving water mass. Once the tide turns, the bottom salinity increases. Because there is a net upstream flow in the bottom waters of

estuaries, any larvae entrained in this higher salinity water mass are carried up the estuary (Wood and Hargis 1971).

Settlement and Juvenile Development

When the pediveliger is fully developed, it extends its foot, makes contact with the substrate, and searches for a filamentous material, such as algae and hydroids (Bayne 1976b). On contact with such a substrate the larva first uses its foot to crawl over the surface or attach loosely (Bayne 1976b). If the substrate is suitable, the larva metamorphoses into the juvenile form, termed a plantigrade, and attaches with byssus threads (primary settlement). The plantigrade remains attached to filamentous substrates until it reaches a length of about 1-1.5 mm. It has been suggested that this primary settlement enables the young mussels to grow in an environment free from the competition for food and space that can occur in dense mussel beds (Thorson 1957).

After growing to about 1.5 mm shell length the plantigrades release themselves from the filamentous substrate and reenter the plankton. The extension of the foot and the attached byssal threads causes the plantigrades to be passively carried by currents in the bottom waters (Bayne 1976b). When the plantigrades contact adult mussels they are stimulated to produce new byssus threads and attach themselves to the substrate, or directly onto the shells of other mussels (Bayne 1976b).

This primary settlement and growth period of the plantigrades, followed by their secondary recruitment into the adult population, makes it difficult to predict exactly when recruitment to any given mussel population will occur (Seed 1976). When this uncertainty is coupled with the wide variation in the time of spawning in different blue mussel populations in the North and Mid-Atlantic Regions, it becomes apparent that recruitment can occur at almost any time of the year.

Adults

The blue mussel lives in habitats that range from flat intertidal shores that drain slowly to vertical surfaces that are subject to much wave splash (Seed 1976). In some localities the penetration of the blue mussel into the sub-littoral zone is limited by the presence of various predators (see Predators section). A primary requisite for the establishment of a blue mussel population is a surface for attachment of the byssus threads; however, the substrate may vary from large boulders to pebbles or, very frequently, other mussel shells. In sheltered environments, large aggregations of mussels sometimes form dense beds that provide shelter and food (in the form of copious amounts of biodeposits) for a variety of other invertebrates. In both these sheltered environments and exposed shores, blue mussel clumps sometimes become so thick that relatively few individuals are attached to the firm substrate. In such situations, storms occasionally wash away large sections of the bed (for review see Seed 1976).

GROWTH CHARACTERISTICS

Blue mussel larvae produced from adults collected from the North Sea and maintained at 12 ^{o}C grew at an average daily rate of 7.5 μm which was reduced to 3.3 μm when the amount of food was decreased by 80% (Sprung 1984). Rate of larval growth increased progressively at temperatures above 5 ^{o}C to a maximum at about 16 ^{o}C. Growth was not reduced by temperatures of up to 20 ^{o}C (Bayne 1965); for larvae from parents collected from a low temperature environment, increases in temperature above 16 ^{o}C reduced growth rates (Bayne 1965). However, as discussed in both the Larval Development and the Environmental Requirements sections, the influence of temperature is not fixed but varies among populations as a balance between genetic composition and previous thermal history.

The size of an adult mussel at any year during its life can be assessed from the annual growth bands that are exposed when the shell is sectioned along the antero-posterior axis (Lutz 1976). These age-length data can be used to construct growth curves to which an exponential equation, such as the generally accepted Von Bertalanffy growth model, can be fitted. Such growth data are available for natural mussel populations from Stony Brook, Long Island, New York (Rodhouse et al. 1986) and Bellevue, Newfoundland (Thompson 1984b). These data (Figure 5) illustrate that the

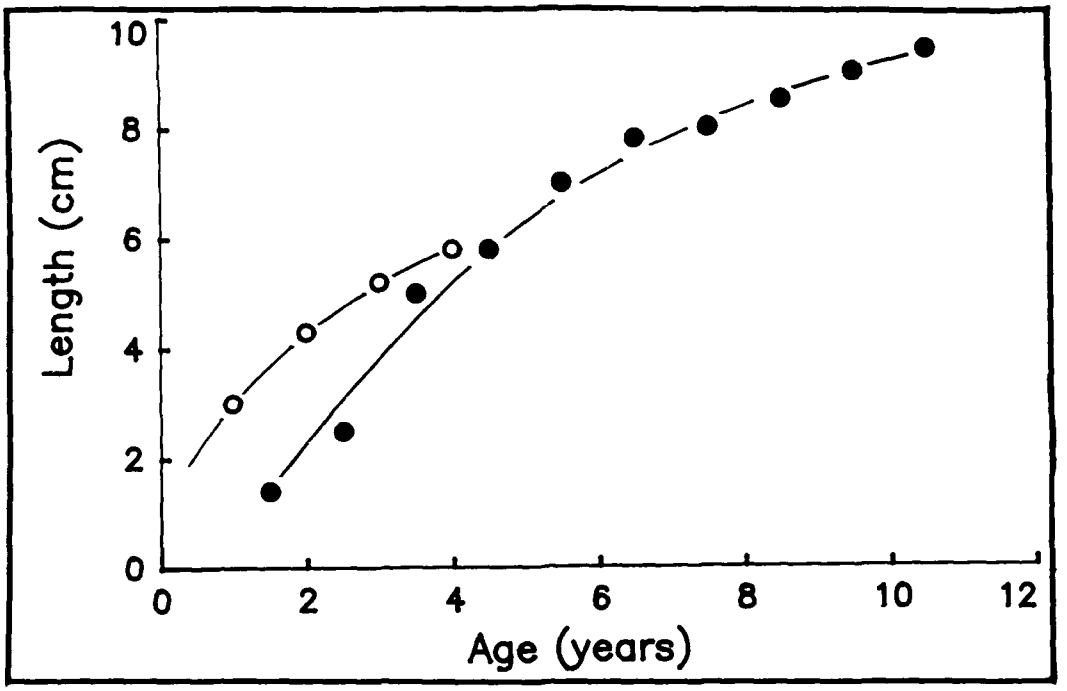

Figure 5. Shell length as a function of age, with the Von Bertalanffy growth model fitted, for blue mussels from New York (open circles; data from Rodhouse et al. 1986) and from Newfoundland (solid circles; data from Thompson 1984b).

southern population has a much faster growth rate for the first two years; however, the maximum age and size attained by mussels is only 4-5 years and 5.5 cm in the southern population but at least 11-12 years and 9.5 cm in the northern population. Such a dependence of growth rate on latitude may possibly be a consequence of the shorter feeding seasons for northern populations; the increased longevity of northern mussels may be a result of reduced metabolism (Seed 1976). On the east coast of the United States the highest recorded growth rates of as much as 5 cm per year (or up to 25 times that in natural populations) were measured in mussels growing continuously submerged in areas of high food availability, such as those in raft-based mariculture operations (Incze and Lutz 1980).

Although shell growth rates are relatively easy and convenient to measure, Thompson (1984b) noted that they are biologically less relevant than estimates of tissue production; he reported that the maximum dry tissue biomass (1.07 kg dry tissue weight $\cdot$ m^{-2}) of a population of blue mussels in Newfoundland developed in June, before a large proportion of the production was spawned as gametes. This estimate is similar to the value of 1.5 $\cdot$ kg m^{-2} recorded by Nixon et al. (1971) for a mussel population in Narragansett Bay, Rhode Island. However, great care must be taken to ensure that when shell growth rates of blue mussels are used to estimate tissue growth that there is no seasonal variation in the allometric relationship between shell growth and tissue growth (Hilbish 1986). Frequently in the blue mussel, as well as in other species of molluscs, the growth of new shell may be disproportionately faster than that of tissue; inaccuracies in production estimates may result. Hilbish (1986) reported that shell growth of small blue mussels (<2 cm shell length) from Long Island Sound, New York, was greatest from April to June, whereas tissue growth was greatest in June and July.

Thompson (1984b) demonstrated that in blue mussels from Newfoundland, the majority of energy was initially partitioned into shell and somatic growth. As the animal grew older, progressively larger proportions of the production was germinal; in the largest mussels, 94% of the assimilated energy was used for the production of gametes. Rodhouse et al. (1986) demonstrated that fecundity was higher in genetically heterozygous than in homozygous blue mussels sharing the same environment.

THE FISHERY

Commercial Shellfisheries

In the United States, the blue mussel has historically not been considered to be as delectable as oysters, scallops, or various species of clams (Clifton 1980); however, due to intensive marketing efforts over the last decade it is becoming an increasingly popular item on seafood restaurant menus throughout the United States. In Canada and Europe the blue mussel is considered to be a quality seafood product and in Spain, France, Holland, and Italy, it forms the basis of an extensive commercial mariculture industry (for review see Mason 1976).

The blue mussel has a number of characteristics that make it ideal for intensive commercial mariculture. The high fecundity and recruitment of natural blue mussel populations allow small mussels to be collected from natural seed beds (Incze and Lutz 1980). The larvae can also be collected directly, at metamorphosis, on fibrous spat collectors that provide the filamentous substrate needed for primary settlement (Mason 1976). Both of these attributes eliminate the need for expensive hatchery production of seed, as required in the oyster mariculture industry of the west coast of the United States. The ability of mussels to attach to surfaces, such as ropes, makes it possible to cultivate them easily 'off-bottom' and not in more complex and expensive suspended racks or cages. This trait is an important benefit to commercial mariculture because it eliminates both self-fouling from the biodeposits (feces and pseudofeces) and the incidence of pearls, and reduces mortality from benthic predators. A detailed analysis of the technical and financial aspects of blue mussel mariculture (Lutz 1980) demonstrated that Mytilus edulis is a good candidate for successful shellfish culture in New England. It grows faster than most traditional shellfish species, yields a higher ratio of meat to total weight, and is nutritionally superior. However, because the market is still relatively limited, intensive mariculture of the blue mussel is only a marginal economic proposition (Clifton 1980).

Currently the economics of the fishery for wild stocks and part-managed bottom culture are much better because per-unit production costs are only about one third those for off-bottom mariculture (Clifton 1980). Although the fishery for wild stocks in New England was thought to be approaching a maximum sustainable yield (Clifton 1980), the discovery of new inshore and offshore beds in Maine and Massachusetts, as well as the development of certain management practices, such as thinning wild stocks and moving stocks between areas to improve meat quality and yields, has enabled annual harvests to increase with demand (Table 2). Blue mussels are generally gathered in the larger commercial operations by dredging and sorting aboard ship using a mechanical washer-grader; in smaller operations they may be harvested in shallow water by raking or pitchforking them into small boats before they are transferred to a larger vessel for mechanical cleaning and sorting (Chalfant et al. 1980).

The blue mussel harvest on the east coast of the United States increased gradually during the decade before 1975 and then rapidly, to more than 1,400 t of meats, in the late 1970's (Clifton 1980). This harvest was the first time the high level of the early 1940's was reached, when the mussel was widely exploited during World War II (Miller 1980). Currently, most of the commercial landings of the blue mussel on the east coast of the United States come from Maine and Massachusetts, and smaller (annually variable) amounts from New York, Rhode Island, and New Jersey (Table 2). The 1986 total harvest of 3,909 t was more than twice as large as that in 1982 and was worth nearly $4 million. The lower average unit value of mussels from Maine, compared with that in other states, is partly due to the fact that a substantial portion of Maine's harvest comes

Table 2. Annual blue mussel landings (metric tons of wet meat weight) and dockside value of the landings (thousands of dollars) for mussel producing states on the east coast of the United States. Years with no commercial harvest are designated by NH. Data provided by National Marine Fisheries Service.

State and item	1979	1980	1981	1982	1983	1984	1985	1986
Maine								
Metric tons	1,361	1,058	1,427	1,315	2,018	2,596	2,762	2,831
Thousands of dollars	716	546	851	835	1,408	1,998	2,079	2,307
Massachusetts								
Metric tons	88	185	296	409	334	328	872	993
Thousands of dollars	107	237	444	511	510	443	1,296	1,441
Rhode Island								
Metric tons	26	45	15	109	NH	NH	58	73
Thousands of dollars	43	29	26	504			258	175
New York								
Metric tons	62	90	51	52	52	67	70	12
Thousands of dollars	72	112	82	81	98	117	118	27
New Jersey								
Metric tons	NH	NH	0.14	0.05	0.41	2.7	NH	NH
Thousands of dollars			0.02	0.08	0.39	4.2		
Totals								
Metric tons	1,537	1,378	1,789.14	1,885.05	2,404.41	2,993.7	3,762	3,909
Thousands of dollars	938	924	1,403.02	1,931.08	2,016.39	2,562.2	3,751	3,950

from unmanaged wild blue mussel beds. The lower meat yield and the high incidence of pearls makes these blue mussels generally inferior to those produced in adjacent managed bottom culture operations. Such differences in quality are mainly due to differences in growth rate, with mussels in natural beds taking over 7 years to attain market size, compared to 2-5 years in managed bottom culture. The higher average value of the wild mussels from Massachusetts and Rhode Island reflects differences in the environmental conditions in these two states that leads to faster growth rates and hence improved meat quality and overall appearance.

There is recreational hand gathering of blue mussels in all states north of New Jersey (Miller 1980); however, little information is available on the size of this fishery because it is subject to much less control (by local ordinances) than are other sport shellfisheries (e.g., for softshell and hard clams). Perhaps one reason the sport fishery is not more important, apart from the lack of public awareness of the blue mussel, is that large numbers of blue mussel beds near population centers are closed because of high coliform counts (Chalfant et al. 1980). In addition, there are public concerns about Paralytic Shellfish Poisoning (PSP), which sometimes results in neurotoxic symptoms and even death in humans (Halstead 1965). This poisoning results from the bioaccumulation by blue mussels (in common with other suspension feeding bivalves, such as scallops and clams) of toxins produced by dinoflagellate algae, especially of the genus Gonyaulax (for a review see Yentsch and Incze 1980). These phytoplankton species, though present throughout the year, undergo periodic blooms during the warmer months, when their numbers increase rapidly. It is only in such situations that the bivalves can accumulate enough toxins to cause PSP. In Maine, New Hampshire, and Massachusetts, state-operated PSP programs use sensitive bioassays to monitor toxin levels in the blue mussel at numerous designated

sampling stations. In this way the mussel beds can be closed to harvest before toxin levels become dangerous (Yentsch and Incze 1980).

Population Dynamics

A large percentage of the eggs spawned by the blue mussel may not get fertilized and large percentages (up to 99) of the larvae that develop may be eaten prior to metamorphosis (Bayne 1976b). Despite this high attrition, blue mussel larvae sometimes are the dominant component of the zooplankton for short periods. Fish and Johnson (1937) reported larval abundances of more than 25 x 10^3 m^{-3} during August in the Bay of Fundy.

The blue mussel has a complex recruitment pattern of primary settlement away from the adult population, followed by almost continual gradual recruitment of the plantigrades into the adult population (Seed 1976). This behavior makes it difficult to assess the mortality patterns of the juvenile stages in a population because it is complicated by immigration and emigration. Thus, the number of plantigrades in a population is seasonally and annually variable, but can range from between 20 to 200 cm^{-2} (Seed 1976).

The mortality pattern of adult blue mussels depends on site-specific environmental factors, such as storms, salinity, temperature, and type of predators (Seed 1976). Thompson (1984b) reported that in a Newfoundland mussel population, mortality was highest during the first 2 years after recruitment. Annual mortality rate was low (5%-16%) at intermediate ages but increased to 91% in blue mussels over 9 years old.

ECOLOGY

Feeding and Nutrition

The blue mussel, both as a planktotrophic larva and as an adult, is an active suspension feeder, deriving its nutrition by filtering organic particles from the water column. Phytoplankton cells are the dominant food source for all life stages (Bayne 1983). Evidence for the role of detritus in the nutrition of the blue mussel is equivocal (Williams 1981), but there is no reason to suppose that non-refractory organic matter is not digested in the same way as living cells (Widdows et al. 1979a). The direct utilization of refractory detritus varies among species of bivalves, but is generally low (Newell and Langdon 1986; Kreeger et al. 1988). Attached bacteria are a major source of protein in detritus (Crosby 1987), and there is evidence that adult blue mussels can digest bacteria (Birbeck and McHenery 1982).

Both larvae and adults use cilia to remove food particles from suspension. The cilia generate a pattern of water flow that creates complex shear velocities which result in small-scale regions of high and low pressure. In the low pressure regions, particles can be entrained in surface water currents generated by other cilia, which then move the particles to oral food grooves (Jorgensen 1981; Jorgensen et al. 1984). The particles, entrapped in mucus secreted within these food groves, are then transported to the mouth.

In larvae, the ciliated velum is used as both a swimming and feeding organ (Bayne 1983). Phytoplankton cells ingested by bivalve larvae must be small (Bayne 1983) because of the physical constraints of the larval esophagus, which is about 10 μm wide. In rearing studies the fastest growth has usually been recorded in larvae fed a mixture of naked flagellates (Bayne 1976b), but little information exists on the natural food of larval blue mussels. Obviously adequate food of a suitable size is essential for the survival and development of larval blue mussels, which have such sharply limited nutrient reserves. Indeed, Sastry (1979) postulated that bivalves may time their reproductive cycle to ensure synchrony between larval development and a suitable supply of food. However, larval mussels can withstand starvation for periods of as long as 10 days (at 16 ^{o}C) without adverse side effects on later development (Bayne 1965).

In adults the gills, which consist of four demibranchs each comprising numerous ciliated filaments, constitute the feeding organ as well as the site for gas exchange. Water enters the mantle cavity through the inhalant siphon and is moved through the ostia (the spaces between adjacent filaments) by the action of lateral cilia. The water exits from the

suprabranchial chamber via the exhalent siphon. The retention efficiency of the gill is high for particles larger than 5 μm, but declines sharply for smaller particles, such that particles smaller than 2 μm are retained with low efficiency (Mohlenberg and Riisgard 1978).

Food particles travel in the oral food grooves to the two pairs of labial palps, which are ridged sorting organs. The palps of bivalve molluscs not only serve to control the total amount of food ingested but also its organic composition (Newell and Jordan 1983), so that the ration ingested by the blue mussel is enriched in organic particles, compared to the particle composition in the water (Kiorboe et al. 1980). The material rejected by the palps, together with some large particles rejected directly by the gills, form aggregates loosely bound in mucus. These pseudofeces are expelled through the inhalant siphon but are close enough to the exhalent siphon to be entrained in the current and carried away (Foster-Smith 1975).

Ingested particles enter the stomach, where they are subject to a combination of enzymatic and mechanical attack from the continuously revolving crystalline style. Particles are also sorted in the stomach, with some particles being channeled by ciliary currents into the digestive diverticula and others, of possibly lower nutritional value and in excess of the capacity of the digestive diverticula to process, constitute the intestinal feces which are removed by ciliary tracts from the stomach into the mid-gut. Particles directed into the ducts of the digestive diverticula are taken into digestive cells by endocytosis and are subject to intracellular digestion for periods of many hours (for review see Bayne et al. 1976a). Assimilated material diffuses into the blood system and the undigested fragments (glandular feces) are ejected into the duct and thence into the stomach and mid-gut. At this point, intestinal and glandular feces are joined into a single mucus-coated fecal ribbon that passes through the anus and is carried away in the exhalent water current.

The volume of water swept completely clear of particles per unit time is termed the filtration or clearance rate. The filtration rate is not constant for any particular weight of mussel, but is infinitely adjustable between zero and a size-dependent upper limit. The actual filtration rate of a mussel at any particular time is the result of a complex balance between endogenous factors (e.g., energy demands and degree of acclimation to environmental variables) and exogenous factors. The only exogenous factor discussed here is the influence of particle concentration; other key environmental determinants of filtration activity (e.g., temperature, salinity, oxygen tension) are discussed later.

The blue mussel is capable of adjusting its filtration rate to maintain a complex balance between the amount of material filtered, the amount rejected as pseudofeces, and the amount ingested (for a detailed review see Bayne and Newell 1983; Bayne et al. 1987). The animal is not stimulated to feed at extremely low particle concentrations (ca. <1 mg $\cdot$ l^{-1}) but filtration increases rapidly with increasing particle concentration. The filtration rate reaches a plateau at particle concentrations of 1-5 mg $\cdot$ l^{-1} and declines to zero only at particle concentrations over ca. 200 mg $\cdot$ l^{-1} (Widdows et al. 1979a). Even though the mussel is capable of filtering large amounts of material from suspension, the amount ingested is finite and depends on gut size (which is a function of body size) and gut residence time. Increasing proportions of the filtered material are rejected as pseudofeces at concentrations above 5 mg $\cdot$ l^{-1}; the ingestion rate is highest at concentrations between 5 and 10 mg $\cdot$ l^{-1} at which point all further material filtered is rejected as pseudofeces. The large amounts of material ingested are first sorted on the palps, ensuring that even in environments with a low ratio of organic food to inorganic particles, the animals ingests predominately organic particles (Kiorboe et al. 1980). Thus, the maintenance of a high filtration rate, followed by efficient particle sorting, is not a wasteful strategy because the energetic costs of filtration are relatively small, whereas those of digesting the food are high (Bayne and Newell 1983). Mussels can compensate for dietary changes by increasing their ingestion rate, absorption efficiency, and the efficiency of the digestive process to help offset decreases in the organic content of the food (Bayne et al. 1987). However, as with physiological adaptations to other environmental perturbations (e.g., temperature)

an acclimation period of about 2 weeks is necessary for the compensation mechanisms to be fully invoked. Thus, such mechanisms are likely to be more important in mediating the mussel's response to seasonal changes in food quality, rather than short-term variations associated with diurnal fluctuations in phytoplankton populations or resuspension of sediment by changes in tidal current velocity.

Predators

Predation pressure on the blue mussel is highest during the 3 weeks when it is a planktonic larva, for it is then subject to grazing from a wide variety of species, ranging from jellyfish to larval and adult fishes. After metamorphosis, predation can limit the distance the blue mussel penetrates into the sublittoral zone (Paine 1971, 1974). Generally predation is highest on the smallest individuals that have the weakest shells. Once a mussel has attained a relatively large and thick shell (4-5 cm) it is vulnerable to attack by only the strongest predators (e.g., large starfish, large crustaceans, and some birds).

In some localities, birds are the most voracious predators of the blue mussel: up to 70% of the net annual production of some mussel populations in Scotland is eaten by birds (Milne and Dunnet 1972). On the east coast of the United States, common avian predators include some species of diving duck (e.g., the common eider Somateria mollissima), various species of gulls, and the American oystercatcher Haematopus palliatus. The aquatic predators are decapod crustaceans, including the American lobster (Homarus americanus), crabs (e.g., Cancer irroratus, Cancer borealis, and Carcinus maenas), starfish (Asterias sp.), whelks (e.g., Thais lapillus and Buccinum undatum), and various fish species (e.g., Tautoga onitis and Tautogolabrus adspersus [Olla et al. 1975]). Because most aquatic predators of the mussel are marine, low salinity estuarine environments provide a refuge from predation for adult blue mussels.

Parasites and Diseases

The blue mussel, in common with other bivalve species, is host to numerous parasites of many species (Lauckner 1983). In only isolated instances have extensive blue mussel mortalities been ascribed to infestation by a parasite. However, off Prince Edward Island, Canada, a haplosporidian tentatively identified as Labyrinthomyxa sp. (Li and Clyburne 1979) did cause extremely high mortalities. Generally the host-parasite relation has evolved to avoid host mortality (Lauckner 1983), although sublethal effects often occur. For example, the trematode Bucephalus sp., which lives in the gonad of the blue mussel, can castrate both sexes. Although castration does not affect the host's survival, it ultimately can compromise the survival of the population by reducing fecundity.

The blue mussel is host to a pea crab macroparasite (Pinnotheres maculatus being more commonly found than P. ostreum [Schmitt et al. 1973]) which lives firmly attached by its rear legs to the gill of the bivalve. In this position, the crab feeds on food particles traveling in the food grooves and can cause severe gill damage, resulting in both a reduction in filtration (Pregenzer 1979) and metabolic rate (Bierbaum and Shumway 1988). Pea crabs are generally confined to sublittoral blue mussel populations south of Cape Cod where, in some populations, infestation rates may be as high as 70% (Schmitt et al. 1973; Bierbaum and Shumway 1988). The spionid polychaete Polydora sp. bores its way into the shell of blue mussel and other molluscs as a refuge. If the polychaete's tube penetrates the inner surface of the shell, the bivalve seals the perforation with a new layer of conchyolin and nacre shell, thus forming a distinct blister (Kent 1979). Blue mussels with heavy infestations of Polydora sp. may have significantly lower tissue weights than those with lighter infestations (Kent 1979).

Competitors

The adult blue mussel on the east coast of the United States is a "competitive dominant," although the juveniles can be in competition for settlement space with barnacles (Seed 1976). Generally, space occupied by blue mussels becomes available for other species only as a result of the removal of entire sections of mussel beds by storms or the elimination of large numbers of animals by predators (Seed 1976). Intraspecific competition is high for the blue mussel due to its

gregarious settling behavior which leads to extremely high population densities (Thorson 1957). Animals within these dense clumps consequently must filter water in which food concentration has been reduced by the feeding activity of neighboring mussels (Wildish and Kristmanson 1984; Frechette and Bourget 1985). Such animals generally do not die, but their growth rate is reduced until they either migrate to the outer edge of the clump (Harger 1968) or the surrounding mussels are removed by other factors (e.g., wave action or predators).

ENVIRONMENTAL REQUIREMENTS

The blue mussel typically inhabits littoral to shallow sublittoral areas in oceanic and polyhaline to mesohaline estuarine environments. Littoral estuarine environments are the most variable of all marine systems in such environmental factors as temperature, salinity, duration of exposure to air, and concentration of suspended particles (Newell 1979). The blue mussel has thus evolved a suite of sophisticated behavioral, physiological, and biochemical adaptations that enable it to survive in such a rigorous environment. These adaptations make it impossible to define for the blue mussel a narrow range of environmental criteria that uniquely describe its habitat. Moreover, the blue mussel is subjected to simultaneous fluctuations in a variety of environmental factors, and its response is to the total resulting stimulus, rather than to single environmental variables. An example of the consequences of such synergistic interactions is that individuals may be able to survive either elevated temperatures or lowered salinities, but cannot survive both perturbations concurrently.

Temperature

The blue mussel along the east coast of the United States cannot establish permanent inshore populations farther south than Cape Hatteras because the adults are incapable of surviving in these waters, where summer water temperatures exceed 27 ^{o}C (Wells and Gray 1960). This temperature closely corresponds with a laboratory estimate of an upper lethal temperature of 27-29 ^{o}C made by Bayne at al. (1977), who also demonstrated that the upper lethal temperature response of the blue mussels depends on the animal's previous thermal history. In mussels acclimated to an intermediate temperature (20 ^{o}C) and transferred to water at 27.5 ^{o}C, the "time to 50% mortality" was 350 h, which was about 8 times as long as that of mussels acclimated to 10 ^{o}C. Tolerance of elevated temperature was also affected by reproductive condition; it was lower in ripe than reproductively quiescent blue mussels. Bayne et al. (1977) also reported that a temperature of 30 ^{o}C was tolerated by small mussels (1-2 cm) twice as long as larger ones (>5 cm).

Blue mussels tolerate low temperatures for extended periods, even to the extent of being frozen in ice for up to 8 months each year in Labrador (Seed 1976). Williams (1970) demonstrated that the animal could not recover if its tissue temperature dropped below -10 to -15 ^{o}C. At lower temperatures more than 65% of the body water freezes, causing irreversible tissue damage. The northward sublittoral distributional limit of the species is not determined by its tolerance of low temperature because sea water never gets colder than about -1.5 ^{o}C. Instead, it becomes limited by the requirement for water temperatures above approximately 5 ^{o}C that last long enough to allow somatic and germinal growth to occur. This fact emphasizes the necessity for understanding how a species responds to typical daily and seasonal temperature fluctuations within its habitat, in addition to understanding its tolerance of environmental extremes in temperature.

Blue mussels are ectothermic organisms, in which tissue temperatures are determined by ambient water or air temperatures. Metabolic processes of the blue mussel are not passively regulated by environmental temperature however, as some rate functions can be adjusted to render them relatively independent of variations in environmental temperature (see review by Bayne et al. 1976a; Newell 1979).

The metabolic responses of the blue mussel to a non-lethal change in temperature have been separated on the basis of the time course of the response (Bayne et al. 1976a). An acute response occurs within the first few hours after an abrupt change in temperature. The response is characterized by an alteration

in rates of oxygen consumption, filtration, etc., which are totally dependent on the magnitude and direction of the temperature fluctuation. If the change in temperature is maintained the acute response is superseded, over an approximately 14-day acclimation period, by a suite of physiological and biochemical adaptations that enable the metabolism to return to near the level prevailing before the temperature changed (reviewed by Bayne et al. 1976a). If the temperature change represents a permanent shift in the environment (e.g., the thermal effluent plume from a power station), the blue mussel population may have to evolve genetically. Such genetic adaptations govern the upper and lower temperature limits.

Widdows (1976) showed that the blue mussel adjusted its filtration rate completely, and metabolic rate partly, to a sinusoidal temperature cycle that varied between 11 and 19 ^{o}C every 24 h. The time course of adaptation was about 14 days, which was similar to the time required for blue mussels to adjust to constant changes in temperature. The final level to which the metabolic rate and filtration were adjusted was similar to these levels in animals acclimated to a constant 15 ^{o}C, and intermediate between the levels recorded for the animals maintained at a constant 11 ^{o}C or 19 ^{o}C.

Thompson and Newell (1985) demonstrated a difference in resporse to temperature between latitudinally separated blue mussel populations. Animals from Long Island Sound, NY, acclimated their feeding rate to temperatures within the range of 5-25 ^{o}C, though their metabolic rate did not acclimate to temperatures above 20 ^{o}C. These southern mussels sustained a positive energy balance, and only 10% died after 26 days, even at the near-lethal temperature of 25 ^{o}C. Mussels from near the northern limits of distribution in Newfoundland acclimated neither their feeding rate nor their metabolic rate to temperatures outside the experimental range of 5-20 ^{o}C. They were so severely stressed at 25 ^{o}C that they did not sustain a positive energy balance and consequently catabolized nutrient reserves; as a consequence, nearly 50% died within 26 days. Thompson and Newell (1985) explained these differences as being due to the differences in exposure to summer water temperatures, which ranged up to 26 ^{o}C in the south but only from 14 to 17 ^{o}C in the north.

Thompson and Newell (1985) suggested that "it is unsatisfactory to define rigidly a particular suite of physiological responses to temperature as characteristic" of a species as widely distributed as the blue mussel. Instead, the response of different populations of the blue mussel to a change in temperature must be viewed as a complex balance between each population's thermal history, food availability, reproductive condition (Widdows 1978), and genetic composition.

Salinity

The blue mussel is a euryhaline species that occurs in environments ranging from full oceanic salinities (34 ppt) to mesohaline (5-18 ppt) estuarine conditions (Bayne et al. 1976a). As discussed in the life history section, the range of salinities that allows normal larval development may be more restricted than the range tolerated by adults. Blue mussels are osmoconforming, i.e., the osmotic pressure of the intracellular fluids is kept isosmotic with the medium by the adjustment of the concentration of free amino acids (Bayne et al. 1976b).

Many estuarine habitats are characterized by fluctuations in salinity associated with the normal ebb of low salinity waters from the estuary and the flood of higher salinity waters back into the estuary. If the tidal variation in salinity is small (< 10 ppt), the blue mussel remains active throughout the salinity fluctuation (Widdows 1985). In response to a rapid drop in ambient salinity, such as may occur with the ebb tide in estuaries with a large input of fresh water, the blue mussel first closes its exhalent siphon to stop the ventilation of the mantle cavity, and then closes its shell if the salinity change is large enough (reviewed by Davenport 1982). It can thus effectively isolate its tissue from up to half the change in ambient osmotic concentration (Shumway 1977). Shell closure cannot be maintained longer than about 96 h (Gilles 1972) because the animal must rely on stored nutrient reserves and anaerobic metabolism to sustain energy demands. If the change in ambient salinity is not a transient event, but represents a longer term change in

environmental conditions, the animal opens its shell and adjusts osmotically to the ambient conditions (Bayne et al. 1976b; Widdows 1985)

The genetic basis of some aspects of the response to salinity change of the blue mussel from populations in the North and Mid-Atlantic Regions have been elucidated (reviewed by Koehn 1983; Koehn and Hilbish 1987). The enzyme aminopeptidase-1 is involved in producing some of the free amino acids that the blue mussel uses to regulate its intracellular osmotic pressure. There are six common allozymes of aminopeptidase-1, all of which have different specific activities. In oceanic blue mussel populations a preponderance of individuals produce the allozyme with the highest specific activity; in low salinity populations most individuals produce the allozyme with the lowest specific activity. Thus, oceanic mussels can more rapidly produce greater quantities of some of the amino acids used in mediating their response to a salinity change. Although larvae from the high salinity populations can settle in estuaries, they die within a few months after settlement (Koehn et al. 1980).

Substrate and Current

The mussel is an epibenthic species that as an adult lives in areas with substrates ranging from rock to coarse gravel; even areas with mud and sand substrates can be colonized provided that there is a firm surface, such as a stone or another mussel shell, to which the byssus threads can be attached. In areas sheltered from fast currents and high energy waves, mussels can build dense beds as a result of their gregarious settlement behavior. Such beds can become unstable as the attachment of the lower mussels to firm surfaces is strained by a large mass of mussels above them. Eventually such dense beds are dislodged by wave action during storms and any mussels that survive have to reattach to available substrate (Seed 1976).

The blue mussel requires sufficient water flow to ensure larval dispersal and carry suspended food particles. It tends to attain a larger size in sheltered environments than in more exposed open coast conditions (Seed 1976). This differential size is probably due to differences in food availability between habitats and the stunting effect of the extensive disturbance of feeding and exposure to air in open coastal populations (Seed 1976). In addition, predation may be so severe in the exposed sea coast populations that few mussels survive into their third year (Seed 1969).

Oxygen

Oxygen diffuses into the blue mussel across the gill, where there is close contact between the water and the hemolymph pumped through the gill filaments by the heart. There are no oxygen-carrying pigments in the blood (Newell 1979). During exposure to air the blue mussel has only a limited capacity to utilize atmospheric oxygen because the valves must be tightly closed to avoid desiccation (Widdows et al. 1979b). During periods of shell closure the oxygen in the water retained in the mantle cavity is used first; thereafter the animal's tissues are subject to hypoxic conditions, and energy requirements are supplied by anaerobic metabolic pathways (Gabbott 1976).

Under certain environmental conditions dissolved oxygen concentrations are reduced in estuarine and coastal waters with restricted circulation, due to the high biological oxygen demand of decomposing organic matter. If the waters become anoxic, the concentration of hydrogen sulfide produced is toxic to many animal species, including the blue mussel. Theede et al. (1969) reported that under laboratory conditions the blue mussel survived 35 days in water at 10 ^{o}C containing only 0.15 ml $O_2 \cdot l^{-1}$, but survival was reduced to 25 days when hydrogen sulfide was present.

In response to a gradual decline in oxygen content, the blue mussel can increase its extraction efficiency for oxygen. Oxygen consumption is thus regulated to be independent of the availability of environmental oxygen (Bayne et al. 1976b). When oxygen availability declines below 60% of saturation, the mussel is unable to compensate by further increases in extraction efficiency. As a consequence, the mussel's oxygen uptake declines rapidly, in direct proportion to the decline in environmental oxygen concentration (Bayne et al. 1976b). Such a decrease in oxygen consumption does not necessitate a reduction in energy production, since anaerobic

pathways are proportionally induced as environmental oxygen levels drop below 90% of saturation (Famme et al. 1981). This use of anaerobic pathways enables the metabolic rate, as measured by heat output, to be sustained near the aerobic rate during brief periods of shell closure or hypoxia.

Anthropogenic Contaminants

The blue mussel has been the subject of innumerable studies of its response to anthropogenic pollutants. Its widespread use for such studies reflects the broad geographical distribution of the species and the fact that it is sessile and intimately exposed to large volumes of water as a result of its suspension feeding activities. The animal is also relatively easy to collect and maintain in the laboratory. The monitoring of physiological and biochemical changes in blue mussels subject to pollution, or the monitoring of chemicals in the tissue, provides a biologically relevant method for quantifying the bioavailability of contaminants in the environment. The use of the blue mussel for this purpose was the objective of the International Mussel Watch Program and Workshop (National Academy of Sciences 1980) which is being continued by the U.S. Environmental Protection Agency. An excellent review of the extensive literature on, and methods for assessing, the effects of stress and pollution on marine invertebrates was compiled by Bayne et al. (1985).

One general conclusion from these studies must be emphasized. Much of the original pollution research was designed to determine the time or concentration of contaminants required to cause a 50% mortality in a test population. Such studies generally involved concentrations that greatly exceeded those commonly found in the environment. Recent studies, pioneered with the blue mussel as a test species, have emphasized the sublethal effects of pollutants. That is, adults might not die, or even be obviously affected, as a result of exposure to a contaminant, but certain aspects of their physiology might be disrupted. If this disruption is prolonged, it can (for example) reduce the energy that individuals have available to partition into somatic and germinal growth. As reviewed in the reproductive strategy section above, any reduction in the nutrient reserves of the egg can reduce larval viability. Thus the stress on the adult is likely to ultimately affect the viability of the population by reducing recruitment.

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15. Supplementary Notes

16. Abstract (Limit: 200 words)

The blue mussel, Mytilus edulis L. is a widely distributed and locally abundant bivalve mollusc in the North and Mid-Atlantic Regions. It is a valuable commercial species; regional landings in 1986 were worth nearly $4 million. It is a semi-sessile species, anchored by byssus threads to firm surfaces in littoral and sub-littoral environments at salinities ranging from 5 to 35 ppt. It is a suspension feeder, ingesting phytoplankton and detrital particles in the size range of 3-30 μm. The geographical range of the species is limited by lethal water temperatures above 27 °C in the south and by temperatures too low for growth and reproduction in the north. Animals from the northern end of the range are stressed by temperatures above 20 °C, whereas those near the southern distributional limit are not severely stressed by temperatures as high as 25 °C. The blue mussel is diecious and oviparous. The planktotrophic larvae take about 3 weeks to develop and metamorphose. The environmental tolerances of larvae are more restricted than those of adults. The juveniles grow to approximately 1.5 mm while attached to filamentous algae before being carried by water currents to reattach to a firm substrate, often close to adult mussels. Larval and adult blue mussels are important prey items for many animals, including crabs, fishes, and birds.

17. Document Analysis a. Descriptors

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Blue Mussel
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